Contribution of environmental and spatial factors to the structure of stream fish assemblages at different spatial scales

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Short title: Scale-dependent contribution of environmental and spatial factors in fish assemblages

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Abstract

To compare the contributions of environmental and spatial factors in structuring assemblages of temperate stream fish on different spatial scales, I evaluated the distance decay of fish assemblage similarity and correlations among species compositions, environmental factors and geographical locations at medium (inter-reach scale, spatial extent 40 km) and fine (inter-microhabitat scale, spatial extent <200 m) scales. Partial redundancy analysis and variation partitioning indicated that the ordinal rank of the relative importance of environmental and spatial factors differed among scales. At the medium scale, the distance decay of similarity of species composition was steep at approximately >10-km scale, and the assemblage structure was simply explained by the distance between sites and several environmental factors (e.g. elevation and current velocity). In contrast, the distance between microhabitats explained only a small portion of the variance in species composition at the fine scale, and fish assemblages were affected by several spatial patterns of habitat (or some environmental features associated with those spatial patterns). Environmental factors at the fine scale (e.g. substratum characteristics and presence/absence of cover) correlated with each other and were spatially structured, and their contribution to species variance was smaller than that at the medium scale. These results provide evidence for scale-dependent alternation of the rank of the relative importance of environmental and spatial factors in structuring assemblages of stream fishes via the turnover of crucially contributing factors from medium to fine

spatial scales.

Introduction

The contribution of ‘environmental factors’ and ‘spatial factors’ in determining community structure is currently an important topic in community ecology. This dichotomy was recently synthesised in a metacommunity theory (Leibold et al. 2004; Cottenie 2005). Leibold et al. (2004) categorised metacommunity theories into 4 paradigms (neutral model, patch dynamics, mass effects and species sorting), questioning whether the structuring of local communities is affected by dispersal limitation, interspecific interactions and habitat heterogeneities. In a river, various biotic and abiotic environments exhibit characteristic spatial structures across multiple scales (e.g. channel networks at the river system scale, directional 1-dimensional structure at the segment scale and environmental patches at the reach and microhabitat scales; Frissell et al. 1986; Montgomery & Buffington 1997) and hierarchical structures are expected to affect both environmental and spatial processes at each scale. Therefore, to evaluate the contributions of environmental and spatial factors in the determination of a riverine community structure, consideration of scale dependency is essential (Holyoak et al. 2005; Heino 2011).

Several studies have examined the contributions of environmental and spatial factors in assemblages of fishes in streams and demonstrated taxonomic or functional group dependency

(Hoeinghaus et al. 2007), the effect of non-native species (Sály et al. 2011), temporal variability (Erős et al. 2012), region dependency (Kautza & Sullivan 2012) and spatial scale dependency. Spatial scale dependency is considered to be the most important factor and has been repeatedly examined (Magalhães et al. 2002; Mykrä et al. 2007; Heino 2011; Sály et al. 2011). However, many previous studies have considered the changes in contribution from large to medium spatial scales (i.e. variation among regions, water systems, segments and reaches) and not from medium to fine scales (i.e. variation among microhabitats).

As with the change from large to medium scales, the contribution of environmental and spatial factors in stream assemblages is also likely to change from medium to fine scales. Previous studies have demonstrated that environmental factors decrease their contribution and spatial factors display the opposite pattern in structuring stream assemblages, with a decrease in spatial scale from large to medium (Magalhães et al. 2002; Mykrä et al. 2007). This trend is a consequence of the large contribution of source–sink effects (mass effects or rescue effects; Amarasekare 2003) at the medium scale and the small (but significant) contribution of biogeographical backgrounds at the large scale (Magalhães et al. 2002). When scaling down from medium to finer scales, the contribution of environmental factors is predicted to be large across all spatial scales via the turnover of corresponding environmental factors, because many previous studies have documented associations between various environmental factors and fish species

68 composition across inter-regional to inter-microhabitat scales (Matthews 1998; Wang et al. 2003;
69 Durance et al. 2006; Heino 2011). In contrast, the contribution of spatial factors is predicted to
70 decline at finer spatial scales because the spatial processes that determine stream assemblage
71 structures strongly associate with the dispersal of individuals that are less constrained by distance
72 at fine scales [e.g. neutral processes at river system scales (Muneepeerakul et al. 2008) and mass
73 effects at reach or segment scales (Falke & Fausch 2010)]. For these reasons, I predicted that the
74 contribution of environmental factors is larger and that of spatial factors is smaller when the
75 spatial scale is decreased (i.e. the reverse pattern of the scale dependency from large to medium
76 scales). However, previous studies on the contributions of environmental and spatial factors in
77 stream assemblages were based on presence/absence data or total individual numbers in reaches or
78 larger sampling units (Magalhães et al. 2002; Mykrä et al. 2007; but see Sály et al. 2011 who
79 compared the presence/absence and relative abundance data at medium and large scales) the scale
80 dependency from medium to fine scale has not yet been examined.
81 Therefore, I conducted a quantitative and detailed investigation of fish distribution and
82 environmental factors at medium and fine scales by direct underwater observations. I predicted
83 that environmental factors would be significant in assemblage structuring at both scales by
84 alternating the responsible factors between the 2 scales. In contrast, spatial factors would be
85 significant only at the medium scale because dispersal constraints among habitat patches would

decrease at the fine scale. Based on the above predictions, the contribution of the environment would therefore increase and the contribution of space would decrease with a reduction in spatial scale. The contributions of individual factors, for both environmental and spatial factors, in assemblage structuring using partial redundancy analysis (partial RDA) were examined. The effects of dispersal processes were also examined by evaluating the distance decay of both species composition and habitat similarity. The contributions of environmental and spatial factors were evaluated using variation partitioning (VP). Based on these results, I demonstrate scale dependency of the contributions of environmental and spatial factors in describing the variance of assemblages of fishes in stream from medium to fine spatial scales and discuss the key processes contributing to assemblage structuring.

Materials and methods

Research area

The study was conducted along the main stem of the Yura River, from the headwater to about 40 km downstream in the lower reaches, in the northern part of Kyoto Prefecture, western Japan (Fig. 1a, b and c). The research area is separated from the lower part of the river by a large dam. The Yura River flows from the Sugio Ridge (750 m a.s.l.), located on the border between Kyoto and

Fukui prefectures, and the river course has a length of about 146 km and a catchment area of about 1880 km^2. The regional climate is warm-temperate with monsoon effects. At the location of the upper quarter of the research area (35°18′N, 135°43′E, 356 m a.s.l.), the annual mean temperature is 11.9°C, annual precipitation is 2298 mm and snow depth in winter is approximately 1 m. The catchment area in the upper part of the research area (0–15 km from the headwater) is covered by conifer plantations of *Cryptomeria japonica* and deciduous broad-leaved forests dominated by *Fagus crenata* and *Quercus crispula* (data from Ashiu Forest Research Station, Field Science Education and Research Center, Kyoto University, http://www.fserc.kais.kyoto-u.ac.jp/asiu/). Residential and agricultural use in the catchment area in the lower part of the research area (15–40 km from the headwater) is less than 5% (data from Nantan City, Kyoto, Japan), and I therefore considered that the effects of these uses on fish species composition were negligible. Artificial protective structures on riverbanks are relatively rare, and most areas of the riverbanks are bordered by forests. Some sediment control dams exist in the middle part of the research area, but all dams have a fishway, and the species composition of fish did not show sudden changes at any dam in a preliminary analysis (see also Results). Thus, I considered that artificial or natural structures restricting dispersal of fishes probably do not exist in the main stream from the headwater to the dam 40 km below.

Hierarchical river habitat structure and spatial scales

The spatial patterns of fish assemblages at medium (inter-reach scale, spatial extent 40 km) and fine (inter-microhabitat scale, spatial extent <200 m) scales were examined. In my research area, the medium and fine scales reflect the inter-reach (intra-segment or intra-river longitudinal) scale and the inter-microhabitat (intra-reach) scale, respectively, in the hierarchical river structure (Frissell et al. 1986; Allan & Castillo 2007). A reach is defined as a repeating sequence of channel units (such as a riffle–pool–run sequence; Frissell et al. 1986; Allan & Castillo 2007). In the Yura River, the length of 1 reach (riffle–pool–run sequence) is approximately 50 m at the upper sites in the research area and 200 m at the lower sites on average.

A microhabitat is recognised as decimetre-scale environmental sets that are patchily distributed within a reach, such as deep locations, boulders, crevices in the bedrock or cover in the riverbank (Frissell et al. 1986).

Sampling sites and observation plots

Twenty-one sampling sites that represented all the river structures contained within the research area were established: sites 1 (uppermost) to 21 (lowest) (Fig. 1c). No sampling sites were established in the river between 4 to 10 km from the headwater because of access difficulties. The Yura River originates from a spring in the forest floor. The uppermost site of the research area was

1.5 km downstream from the origin. The lowest sampling site was located just upstream of the dam reservoir.

Ten line transects were set perpendicular to water flow along the channel at each sampling site (Fig. 1d). The interval between transects was adjusted according to river size: 5-m intervals at the upper 4 sites (sites 1–4); 20-m intervals at sites 14, 20 and 21 and 10-m intervals at all other sites. Each sampling site included at least 1 reach (1–3 reaches). Plots were established along each transect at regular intervals (4–8 plots per transect; Fig. 1d). Plots were the minimum unit of observation and measurement. The number of observation plots along the transects was adjusted according to channel width: 4 plots at the upper 4 sites (sites 1–4; mean wet width <5 m), 8 plots at sites 14, 20 and 21 (mean wet width >20 m) and 6 plots at the other sites (mean wet width 5–20 m). A red-coloured sounding lead was placed at the centre of each observation plot as a landmark for fish observation and environmental measurements.

Fish observations

Fish observations were conducted in the summer from 20 August to 27 September 2009. During this season, the water temperature of the river is at its annual maximum, and all fish species are active (Nakagawa, unpublished data). Observations were conducted by snorkelling during the day (10:00–15:00) and night (22:00–3:00), because some fish species are active at night. Water

158 temperature was measured at the start time of each observation. Snorkelling observations were
159 conducted by the line-transect method using the following procedure: First, I dived into the right
160 or left side of a stream channel and moved to 1 m downstream of a transect. Five minutes later, the
161 fish showed normal behaviour, I quietly moved along the transect and observed the fish. When an
162 individual fish was found, I recorded its species and the nearest landmark lead. All observations
163 were conducted by the same person (HN). The observation time was approximately 20 min
164 (including waiting time) per transect. A waterproof hand light and headlight were used for night
165 observations. Because diet and habitat shifts during larval and juvenile periods occur in some
166 target species (Nakamura 1969), data for larval fish were excluded from the analysis.
167 The number of individuals of each species observed at a plot at each sampling site (4 plots at
168 sites 1–4, 6 plots at sites 5–13 and 15–19 and 8 plots at sites 14, 20 and 21) was used to determine
169 fish distribution data at the fine scale. In the research area, 27 fish species were observed in total
170 (Nakagawa, unpublished data). Although the bluegill sunfish, *Lepomis macrochirus*, was
171 introduced from North America, this species was included in the analysed data set because it
172 became established in this river at least 14 years prior to the study (National Census on River
173 Environments of Japan 1993); hence, its distribution is not likely to be restricted by its initial
174 location of introduction. The largemouth bass, *Micropterus salmoides*, was also introduced from
175 North America, but I did not observe this species in the research area, probably because it is

primarily lentic and restricted to dam reservoirs. *Anguilla japonica*, *Plecoglossus altivelis* and *Oncorhynchus masou* were excluded from the analysed data set as they are introduced annually by a local fishery cooperative, and I could not determine the innate distribution of these species. Among the material species in this study, *Zacco platypus*, *Cyprinus carpio*, *Carassius auratus* and *L. macrochirus* occupy the dam reservoir (National Census on River Environments of Japan 1993); however, *Z. platypus* mainly occupies stream habitats (Nakamura 1969), and the other species are rare in the upper to middle reaches of the Yura River (see Results). Therefore, the effect of the dam reservoir seems to be small in this research. The total number of individuals of each species at each sampling site was used for fish distribution data at the medium scale. Day and night data were pooled.

Environmental data

Environmental factors were categorised into medium- and fine-scale descriptors on the basis of previous studies that referred to the spatial scales critical for habitat selection by fish (Table 1). For example, in general, water temperature gradually increases from upper to lower reaches at the kilometre scale, and therefore the distribution of a fish species determined by temperature tolerance would be responsive at this scale (Fausch et al. 1994). Water temperature was therefore categorised as a medium-scale factor. Pinpoint habitat patches such as cover and boulders are used

as short-term habitats for refuge or foraging sites (Sechnick et al. 1986; Fuselier & Edds 1995; Nakagawa et al. 2012); thus, these were considered fine-scale factors.

Fine-scale data (i.e. water depth, current velocity, substratum characteristics and presence/absence of cover) were measured at the point of each landmark lead (i.e. each observation plot) after fish observations. Water depth was measured with accuracy of 1 cm using a metre stick. Current velocity was measured at 60% water column depth using a portable tachometer (Model 3651 Pocket Tachometer, Cosmo-Riken, Osaka, Japan). To measure substrate characteristics, a 50 × 50-cm quadrat with 10 × 10-cm cells (total of 25 cells) was placed on a landmark. Furthermore, the major substrate type was recorded, which was characterised by sediment particle size, in each cell based on the Wentworth–Udden particle scale (<2 mm, sand; 2–4 mm, granules; 5–64 mm, pebbles; 65–256 mm, cobbles; >256 mm, boulders; bedrock; Wentworth 1922). Cover was defined as over-hanging branches and leaves of terrestrial plants that were more than 50 cm long.

A portion of the medium-scale data was calculated as the mean of measurements for all observation plots or transects included in each sampling site. This method was applied for water depth, current velocity, substrate characteristics, presence/absence of cover and channel width. The other portion of medium-scale data (the gradient of the river bed at each sampling site) was obtained from a 1:25,000 map published by the Geospatial Information Authority of Japan. The

gradient of the river bed was represented as the mean of 30 gradient measurements for 100-m intervals within ±1.5 km of the upper and lower reaches around the sampling site. Water temperatures measured at each observation were averaged. Flow rate was calculated as the product of the means of water depth, current velocity and channel width at each sampling site.

Spatial data

Spatial variables at each spatial scale were constructed using Moran's eigenvector mapping (MEM) technique. MEM describes the spatial structures of species composition by the eigenvalues and eigenvectors that represent the spatial relationships between sampling points across various spatial scales (Dray et al. 2006). The MEM approach offers advantages over direct geographical coordinate or trend-surface (i.e. polynomial) approaches in that MEM ensures independence between spatial variables and detects wider-range spatial structures. These methods have been reviewed in detail by Okuda et al. (2010) (see also Borcard & Legendre 2002; Borcard et al. 2004; Dray et al. 2006).

Spatial patterns of the observed assemblages were analysed separately for the medium and fine spatial scales. For the medium scales, the 21 sampling sites on the main stream were approximated by points on a 1-dimensional line, such that the order and interval of the points reflected the location of the sampling sites (see upper figure in Appendix 1). For the fine scale,

disposition of the observation plots was approximated in each sampling site by 10 × 4 grids with a 10:1 aspect ratio at the upper 4 sites (sites 1–4); 10 × 8 grids with a 10:1 aspect ratio at sites 14, 20 and 21; and 10 × 6 grids with a 10:1 aspect ratio at the other sites (see the lower figures in Appendix 1). A spatial weighting matrix (SWM) was constructed for the medium-scale data and 21 SWMs for the fine-scale data from the distances of neighbouring sampling sites and then from the distances from each of the neighbouring observation plots within a sampling site, respectively (Dray 2010). Moran's eigenvectors (MEVs) were calculated from an SWM and used as the spatial variables. An MEV exhibited a wave-like spatial pattern when plotted on the location of the sampling sites or observation plots (see Results) and represented the autocorrelation patterns of these sites and plots (Dray 2010).

Tests of distance decay in fish assemblages and environmental similarities

The similarity indices of species composition and habitat characteristics were calculated between sampling sites at the medium scale and between observation plots at the fine scale to analyse the decay of these similarities with distance. The distance was defined as the straight-line distance between pairs of observation plots at the fine scale and as the distance along the river between pairs of sampling sites at the medium scale. At the fine scale, similarities between <5 m and >50 m distant plots were eliminated from the analysis because they did not exist in common at all

sampling sites. The Bray–Curtis similarity index (1− the Bray–Curtis dissimilarity), based on the number of individuals of each species at sampling sites or observation plots, was used to express the similarity of species composition. The correlation between the similarity of species composition and distance was examined using Mantel tests at each scale. The environmental characteristics measured at the medium and fine scales (Table 1) were used to calculate the habitat similarity at each scale. For evaluating habitat similarity, principal components analysis was conducted on the basis of the environmental characteristics for each spatial scale and obtained principal component (PC) scores of observation plots for PC 1–4 at the medium scale and PC 1–5 at the fine scale; these explained >80% of the total variance in environmental characteristics for each spatial scale. Subsequently, the multidimensional Euclidian distance (D) of the PC scores was used to calculate the index of habitat similarity. By using the transformation $1-D/(1+D)$, D has been converted into a similarity index ranging from 0 to 1. The correlation between habitat similarity and distance was examined using Mantel tests at each spatial scale.

Multivariate analysis

In the multivariate analyses of VP procedure, the Hellinger transformation (rows of the data set are standardised by their row sum and then a square root transformation, Legendre & Gallagher 2001) was applied to data for species composition in each plot or each site to adjust the difference in the

size of observation units and avoid the horseshoe bias (Peres-Neto et al. 2006). VP analysis was conducted to evaluate the contributions of environmental and spatial factors in determining spatial patterns of assemblages at different spatial scales. The total variation contained in the distribution data for fishes was segregated into unique environmental and spatial components using redundancy analysis (RDA) based on a VP approach (Borcard et al. 1992). RDA is a constrained ordination technique and serves as a multivariate extension of linear regression analysis (Legendre & Legendre 1998; Beisner et al. 2006; Okuda et al. 2010). The environmental variables were log-transformed (Stewart-Koaster et al. 2007; Erős et al. 2009). A forward selection technique was conducted according to Blanchet et al. (2008) before RDA for the environment and spatial variables to find the statistically relevant variables. VP was calculated from 3 RDAs as follows. The first RDA uses sets of both environmental and spatial variables and obtains the total variation of a distribution data for fishes explained by environmental and spatial variables, expressed as [E + S]. The second RDA calculates the fraction [E] that is explained by environmental variation, involving co-effects of spatial variables. The third RDA calculates the fraction [S] explained by the spatial variation, including co-effects of environmental variables. [E + S], [E] and [S] were adjusted for a multiple coefficient of determination ($R^2_{adj.}$) according to Peres-Neto et al. (2006). Note that, in some cases (e.g. small sample size, large number of explanatory variables), negative values can be obtained. The other fractions can be obtained as follows: the fraction of variation

284 explained by environmental factors independent of spatial factors is [EP] = [E + S] − [S], the
285 fraction of variation explained by spatial factors independent of environmental factors is [SP] = [E
286 + S] − [E], the fraction of variation explained by correlations between environmental and spatial
287 factors is [ES] = [E] + [S] − [E + S], and the residual fraction of variation is [R] = 1 − [E + S].
288 [EP] and [SP] indicate the independent effects of observed environmental conditions (associated
289 with niche explanations) and spatial arrangement (representing local dispersal processes or an
290 environmental factor associated with that spatial pattern), respectively, in determining the spatial
291 variation in species composition. [ES] represents the fraction explained by variables that cannot be
292 statistically divided into environmental and spatial factors (Peres-Neto et al. 2006). [R] is the
293 unexplained spatial variation in species composition and includes the effects of unmeasured
294 environmental factors and stochastic mechanisms. The VP approach has the potential risk of
295 underestimating the relative contributions of environmental factors when important environmental
296 factors are not included in the data set (Gilbert & Bennett 2010; Smith & Londholm 2010). For
297 example, river-bank characteristics were not included as environmental factors because of their
298 explicit correlations with the spatial arrangements of observation plots. Therefore, possible
299 spurious correlation of a spatial factor must be considered when interpreting the results of VP
300 (Gilbert & Bennett 2010; Smith & Londholm 2010). However, despite this problem, the VP
301 approach is a good tool in the first step of partitioning out environmental and spatial components

from the total variation in species composition using appropriate adjustments [e.g. the unimodal distribution of species (Peres-Neto et al. 2006; Legendre & Gallagher 2001), the inflation of variance (Blanchet et al. 2008) and sampling density (Peres-Neto et al. 2006)].

The significance of the testable variance fractions (i.e. [EP], [SP] and [ES]) was tested using permutation tests with 9999 randomisations of the correspondence between the spatial patterns of species composition and each set of environmental and spatial predictors according to the tutorial of the statistical software CANOCO (Borcard et al. 1992; Leps & Smilauer 2003). For each spatial and environmental predictor at the fine scale, significance was also tested for each sampling site because the selected predictors differed among sites. *P*-values were adjusted by the number of variables in each VP or partial RDA using the Bonferroni method.

Forward selection of variables, VP, permutation tests, partial RDA and MEM were performed using the statistical software R (R Development Core Team 2010) with the add-on packages ‘vegan’ (Oksanen et al. 2008), ‘spacemakerR’ (Dray 2010) and ‘packfor’ (Blanchet et al. 2008).

Results

Fish species composition and its distance decay

A total of 9520 individuals of 27 fish species were observed, and data for 9402 individuals of 24

species were used for analyses (Appendix 2). Uneven distribution patterns biassed towards the upper, upper-middle, lower-middle or lower reaches at the medium scale were observed in some fish species; thus, species composition changed along the river course (Fig. 2). Several fish species exhibited bell-curve-like patterns of distribution, having a centre of distribution with high population density at a certain position in the river course and a skirt of distribution with low population density (Fig. 2).

Similarity in species composition was significantly correlated with the distance at the medium scale (Mantel test, $r = 0.772$, $P = 0.001$, Fig. 3a) but not at the fine scale ($r = 0.014$, $P = 0.424$, Fig. 3b). The decay of species similarity was particularly clear at 10 km or larger scales (Fig. 3a).

Habitat environments and their distance decay

In general, at the medium scale, water temperature, gradient of the river bed, flow rate and mean width of the river channel simply decreased or increased from upper to lower reaches. In contrast, other factors (e.g. mean water depth and mean current velocity) did not demonstrate such simple patterns along the upper–lower locations of the river (Appendix 3). Distance decay in similarity of habitat environment was detected at both the medium scale (Mantel test, $r = 0.629$, $P = 0.001$; Fig. 3c) and the fine scale (Mantel test, $r = 0.075$, $P = 0.040$; Fig. 3d), but the effect was much weaker

for the latter. In contrast to the distance decay patterns in species composition similarity, habitat similarity was nearly constant around the 10–20-km spatial scale.

Partitioning of environmental and spatial factors and significance of individual factors

I obtained data sets for species composition at the fine scale, environmental variables and spatial variables at 1063 observation plots, excluding plots where no fish were observed. According to the VP analysis, the predictor variables explained 85.98% of the total variation in species composition at the medium scale and the mean variation of 36.5% at the fine scale (Tables 2 and 3).

At the medium scale, 3 environmental variables (elevation, water temperature and mean current velocity) and 6 spatial variables (MEV 1–6) were selected (Table 2). At the fine scale, the number of selected environmental variables was 2 at site 18, 1 at sites 2, 3, 6, 7, 9, 11–15 and 21 and none at the others (Table 3). The number of selected spatial variables varied from 1 to 13 among sites (Table 3).

The fractions of variation explained by pure environmental predictors [EP], pure spatial predictors [SP] and by both environmental and spatial predictors [ES] changed with the spatial scale (Tables 2 and 3). The results of permutation tests indicate the significance of [ES] at both scales, but [ES] explained a larger fraction (68.2%) at the medium scale compared with the mean value of the fine scale (4.2%). In each site examination at the fine scale, [ES] was significant at 10

of the 21 sites. [SP] explained the largest portion (31.5% of the mean) at the fine scale and the second largest portion (12.6%) at the medium scale and was significant at both scales. At all sampling sites, with the exception of site 14, [SP] significantly explained the variation in species composition at the fine scale. [EP] explained a relatively small portion of the variation at both scales (5.2% and 1.0% of the mean at the medium and at the fine scales, respectively) and was significant only at the medium scale. [EP] was significant at 3 of 21 and 7 of 21 sites with and without Bonferroni adjustment.

The results of partial RDA excluding the effect of spatial variables indicated a significant effect of elevation and mean current velocity at the medium scale (Table 2). At the fine scale, the significance of individual variables (water depth, current speed, several substrate characteristics or presence/absence of cover) was indicated at 6 of 21 sites, but a consistent pattern among sites was not detected (Table 3). The elevation and mean current velocity at the medium scale, water depth, current speed, several substrate characteristics and the presence/absence of cover at the fine scale were significantly correlated with the number of individuals of several fish species in sampling sites or observation plots (general linear model, $P < 0.05$; see also Appendix 4).

The results of partial RDA excluding the effect of environmental variables indicated significant effects of MEVs 1, 2 and 3 at the medium scale (Table 2). MEVs 1, 2 and 3 exhibited fluctuating patterns, with wavelengths ranging from approximately 10 to 20 km (Fig. 4). Their

374 peak positions and fluctuating patterns corresponded well with the distribution of some fish
375 species (e.g. MEV 1 was significantly correlated with the distributions of *Zacco temminckii*,
376 *Pungtungia herzi* and *Squalidus gracilis*; r^2 = 0.58, 0.55 and 0.51, respectively; all $P < 0.001$; Figs
377 2c and 4).

378 At the fine scale, the number of significant spatial variables ranged from 0 to 2 and 0 to 6
379 with and without Bonferroni correction, respectively, in the partial RDA (Table 3). Three spatial
380 variables commonly explained a large proportion of the variation in species composition across
381 several sites (MEV 2 at sites 6, 8, 10, 12 and 19; MEV 4 at sites 12 and 16–19 and MEV 45 at
382 sites 5–8, 10, 13, 17 and 18). These spatial variables exhibited characteristic spatial patterns, i.e.
383 horizontal patterns relative to a river channel for MEVs 2 and 4 or patch-like patterns for MEV 45
384 (Fig. 5).

385

386 **Discussion**

387 *Scale dependency of the contribution of environmental and spatial factors across medium to fine*
388 *scales*

389 Contrary to my original prediction, the results of VP analysis indicated the contribution of spatial
390 factors associated with the distance between sites or an arrangement of local habitats in the
391 determination of fish species composition at both the medium and fine spatial scales in the middle

to upper Yura River. Results at the medium spatial scale were consistent with those of previous studies in which dispersal processes such as dispersal limitation, mass effects and patch dynamics played key roles in determining the distribution of several species of stream organisms (Cottenie 2005) and fish communities in a river (Magalhães et al. 2002; Falke & Fausch 2010; Winemiller et al. 2010). However, in the present study, the distance decay of the similarity of species composition was steeper at the medium scale (especially ≥10 km) than that at the fine scale. These results indicate that the dispersal of fish individuals was strongly determined by the distance between local habitat patches at the medium scale. The differing patterns observed for the distance decay of species composition and that of habitat characteristics at the medium scale also support dispersal processes rather than habitat selection of fishes. The distance decay of species composition at medium spatial scales (spatial extent about 4–50 km) has also been reported in several stream fish assemblages (Magalhães et al. 2002; McGarvey & Ward 2008). In contrast, the practically negligible distance decay at the fine scale indicates that distance between microhabitats explained only a portion of the contribution of spatial predictors in structuring assemblages. Several fine-scale spatial predictors showed 2-dimensional patterns (i.e. horizontal patterns relative to a river channel and patch-like patterns) that were significantly associated with the variation in species composition at several sampling sites. This result may be related to the home ranges of fish as discussed in the next section.

410 The contributions of environmental predictors in explaining fish assemblages were
411 significant at medium spatial scales when the effect of correlations with spatial predictors was
412 removed. This finding supports classical niche theories, such as habitat template theory
413 (Southwood 1977; Townsend & Hildrew 1994) and species sorting theory (MacArthur 1958;
414 Pianka 1966), in which interspecific variation in habitat niches is considered a key factor in
415 structuring communities at medium scales. In contrast, the variation of assemblage structures
416 explained by environmental factors was small at the fine scale, and the largest part of that could
417 not be divided into environmental and spatial factors. Subsequently, in the forward selection of
418 environmental variables, only 1 variable was selected at most sampling sites. These patterns
419 indicate that environmental gradients of microhabitats in a reach were strongly spatially structured
420 and correlated with each other. Therefore, in contrast to the medium scale, pure environmental
421 processes may explain only a limited part of the assemblage structure of stream fishes at the fine
422 scale. The scale dependency of the contribution of environmental factors in the determination of
423 fish distribution has been reported for individual species across various spatial scales (Fausch et al.
424 1994; Inoue et al. 1997; Perkin & Gido 2011), but for fish assemblages, only large to medium
425 scales have been considered and not medium to fine scales (Wang et al. 2003; Durance et al.
426 2006).
427

Processes determining species composition at each spatial scale

1. *Medium scale*

At the medium scale, the spatial variation in species composition was largely explained by distance, reflecting the distance decay of species composition and bell-curve-like distribution along the river course for some fish species. These patterns are typically caused by dispersal constraints of individuals by distance or an environmental factor that is strongly structured spatially (Peres-Neto et al. 2006). Although the further concern about the effect of unmeasured and spatially structured factors is needed, these results might support previous findings indicating the importance of source–sink effects not only in the population dynamics of individual species but also in the assemblage determination of stream fishes (Falke & Fausch 2010). Source–sink dynamics are an aspect of metacommunity dynamics, in which dispersal from a large source population of component species maintains small sink populations in neighbouring local communities that cannot be maintained by self-reproduction and would become extinct without immigration from other local communities (Amarasekare 2003). Dispersal of individuals from a source population maintains a sink population of a species, which helps to increase the local richness and diversity of species (Amarasekare 2003; Holyoak et al. 2005). In the present study area, no artificial structures were present that strongly restricted fish dispersal. However, if any artificial barriers, such as a sediment control dam without a fishway, are constructed and restrict

the free movement of fish, sink populations may become extinct (Jager et al. 2001), and the richness and diversity of local fish assemblages may decrease (Stewart et al. 2001). My results re-emphasize the importance of river connectivity in maintaining the species diversity of fishes, which is a crucial issue for stream fish conservation (Nilsson et al. 2005).

Independently and along with the spatial predictors, the environmental predictors of elevation and mean current velocity significantly explained the variation in species composition at the medium scale. In addition, the local density of several fish species was significantly correlated with mean current velocity within a reach. This variable changed within a spatial extent of <10 km. Within this spatial range, the distance decay in species composition was not steep. Previous studies on single fish species showed that fish select a reach with a favourite current velocity within a scale for which the migration of individuals is not prevented (Table 1). The effect of habitat selection along environmental gradients on assemblage structuring may be strong at the <10-km scale; thus, a shifting point of the rank of the relative importance of environmental and spatial factors may exist within the medium scale (400–40,000 m).

2. *Fine scale*

At the fine spatial scale, contrary to my prediction, the variation in species composition was significantly associated with spatial predictors at all sampling sites, with the exception of site 14

but was not simply explained by the distance. In contrast, environmental predictors explained a relatively small portion of the total variation in species composition, although the environmental factors significantly affected species composition at several sites at the fine scale.

In the situation where an environmental factor at medium or large spatial scales strongly constrains the ecological traits of stream fishes, the contribution of environmental factors may be small because of decreased interspecific variation in habitat selectivity (Grossman et al. 2010). In general, environmental harshness seems to be stronger in the upper reaches than in the lower reaches (Grossman et al. 2010), so it is predictable that the contribution of environmental factors will be small in the upper reaches and large in the lower reaches. However, the fraction explained by environmental variables was not large in the lower reaches, but it was large at 2 sites in the upper reaches (Table 3). In addition, a previous study reported the interspecific variation in habitat use of the dominant fish species in the upper middle reaches of the research area (Nakagawa et al. 2012). Therefore, the effect of an environmental factor probably does not explain the small contribution of environmental factors in the assemblage structuring of stream fishes at the fine scale.

To simultaneously explain both the large contribution of spatial factors and weak habitat selectivity, a dispersal process at the fine spatial scale may need to be considered. This process may be associated with the home range of individuals. Several significant environmental features

(deep pool, cobbles, crevice of bedrock and cover) usually function as a refuge or rest site (Table 1) and may be used as a core site within the home range of individual fish (usually smaller than a few hundred metres for fish of <50 cm standard length; Minns 1995), as shown in studies of stream and marine fishes (Miller & Geibel 1973; Lowe et al. 2003; Jorgensen et al. 2006; Watanabe 2008). When fish use a particular environmental patch as a core site within their home range, some environmental factors will exhibit relationships with the distribution of that fish species. On the other hand, in situations where fish limit their movement within a fixed area independently of environmental gradients around a core site, some spatial factors would also exhibit relationships with the distribution of that fish species. This situation would also affect species composition because of spatial autocorrelation in individual species density that relates to the core site distribution. Horizontal and patch-like patterns of spatial predictors that are significantly related to fish distribution may corroborate the importance of the home range and associated core sites in structuring fish assemblages.

Concluding remarks

The present study successfully demonstrated that the ordinal rank of the relative importance of environmental and spatial factors changes between 2 spatial scales via alterations of multiple, scale-dependent factors. However, large portions of the variation in species composition could not

be statistically attributed to either environmental or spatial factors. Furthermore, potentially important environmental factors that were not included in the analysis may have resulted in spurious correlations between species composition and spatial factors, such as primary production (Vannote et al. 1980) or interspecific interactions (Hutchinson 1959; MacArthur & Levins 1967; Amarasekare 2003). In future studies, I hope to strictly evaluate the effect of significant factors using multi-site comparisons (Didham et al. 1998; Brown and Swan 2010) or environmental control experiments (Eggleston and Lipcius 1992; Everett and Ruiz 1993). If the large contributions of spatial factors and distance decay are caused by source–sink dynamics in a river that is fragmented at a scale smaller than 10 km by natural or artificial structures, the contribution of spatial factors will be smaller than that in a non-fragmented river, and the distance decay of assemblage similarity will be steep at a smaller scale. Furthermore, if the home range of individual fish affects assemblage structuring, the distribution of fishes will be explained by the distance from the home-range core. This prediction may be testable with experiments using artificial removal/placement of microhabitats functioning as home-range cores (e.g. cover or boulders).

The implication that fine-scale assemblage structure may be determined by factors that change at a medium or larger spatial scale has an important meaning for the conservation of species diversity in stream ecosystems. When conducting environmental assessments, if a prediction concerning a certain effect is based on data that were only sampled within a planned

518 construction area (i.e. data that do not include factors changing at a larger spatial scale), the
519 assessment risks bias or misinterpretation (Roth et al. 1996). In the future, knowledge of current
520 community ecology that considers multiple-scale processes will be increasingly essential for
521 management decisions regarding modification or maintenance of stream environments.
522

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536

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748 Table 1. Environmental factors measured along the Yura River study site and associated

749 mechanisms that determine community structure

750

Measured environmental factor	Ecological importance	Spatial scale
Water temperature	Thermal tolerance (e.g. Elliott 1981, Fausch et al. 1994)	Medium scale
Gradient of riverbed	A determinant factor of river morphology (e.g. Montgomery and Buffington 1997, Quist et al. 2004)	Medium scale
Flow rate	A determinant factor of river morphology (e.g. Buffington et al. 2003)	Medium scale
Mean width of river channel	An indicator of the canopy cover which affects primary production in a river (e.g. Hill et al. 2001)	Medium scale
Mean water depth of a research site	An indicator of the frequency of refuges for predators (e.g. Power 1984)	Medium scale
Mean current velocity of a research site	An indicator of the frequency of a lentic habitat (such as pools) which are used for foraging or resting (review in Fausch et al. 1988; e.g. Quist et al. 2004) A determinant factor of density of reproductive nests (e.g. Natsumeda 2001)	Medium scale
Mean frequency of each substrate type in a research site	An indicator of the frequency of habitat patches for feeding or spawning (review in Fausch et al. 1988, Mills 1991, Wooton 1998, e.g, Inoue et al. 1997, Quist et al. 2004) A determinant factor of the density of feeding site or reproductive substrate for some Japanese fishes [e.g. sand for Zacco platypus, Pseudogobio esocinus and Hemibarbus labeo (Nakamura 1969); gravel for Tribolodon hakonensis (Nakamura 1969); cobbles for Rhinogobius spp., Tridentiger kuroiwae and Chaenogobius urotaenia (Kawanabe and Mizuno 1989, Tamada 2010); boulders for Pseudobagrus nudiceps, Liobagrus reinii and Cottus pollux (Yamane 2004, Watanabe 1994, Natsumeda 2001, Nakagawa et al. 2012)]	Medium scale
Mean cover frequency of a research site	A determinant factor of the density of feeding sites, shelter and reproductive substrate (e.g. Shirvell 1990, Inoue et al. 1997) Reproductive substrate for some Japanese Cyprinids; Squalidus gracilis, Carassius auratus (Nakamura 1969)	Medium scale
Water depth at a plot	Refuge of predators (e.g. Power 1984)	Fine scale
Current velocity at a plot	A factor affecting foraging efficiency (e.g. Hill and Grossman 1993, Nakano 1995)	Fine scale
Frequency of each substrate type at a plot	Feeding site for some benthic feeders (review in Lamments and Hoogenboezem 1991) Shelter from predator or high current speed (e.g. Fuselier and Edds 1995; review in Matthews 1998) Feeding site or shelter for some Japanese fishes [e.g. sand for Pseudogobio esocinus, Squalidus gracilis and Hemibarbus longirostris (Nakamura 1969); Boulders for Pangtungia herzi, Niwaella delicata, Pseudobagurus nudiceps, Liobagurus reinii and Cottus pollux (Nakamura 1969, Kawanabe and Mizuno 1989, Nakagawa et al. 2012)]	Fine scale
Cover present/absent at a plot	Shelter from predator or high current speed (e.g. Sechnick et al. 1986, Shirvell 1990)	Fine scale

751 Table 2. Portion of variation ($R^2_{adj.}$) explained by pure environmental variables [EP], pure spatial
752 variables [SP], both environmental and spatial variables [ES], the total of environmental and
753 spatial variables [T] and the residual fraction of variation [R] estimated by variation partitioning
754 (VP), and that explained by each pure environmental variable and pure spatial variable (Moran's
755 eigenvector, MEV) obtained from partial redundancy analysis (partial RDA) at the medium scale.

	$R^2_{adj.}$	P-Value
EP	0.052	**< 0.001**
SP	0.126	**< 0.001**
ES	0.682	**< 0.001**
T	0.860	
R	0.140	
Environmental factors		
Elevation	0.025	**0.009**
Water temperature	0.011	0.208
Mean current velocity	0.020	**0.024**
Spatial factors		
MEV1	0.042	**0.034**
MEV2	0.056	**0.004**
MEV3	0.056	**0.003**
MEV4	0.015	0.517
MEV5	-0.007	1.000
MEV6	-0.002	0.565

Table 3. Portion of variation ($R^2_{adj.}$) explained by pure environmental variables [EP], pure spatial variables [SP], both environmental and spatial variables [ES], the total of environmental and spatial variables [T] and the residual fraction of variation [R] estimated by variation partitioning (VP), and that explained by each pure environmental variable and pure spatial variable (Moran's eigenvector, MEV) obtained from partial redundancy analysis (partial RDA) at the fine scale. Mean ± SD in the left column shows the average and standard deviation of [EP], [SP], [ES], [T] and [R] among all sampling sites. Dashes (–) represent unselected variables by forward selection. MEVs that were not selected at any sampling sites were omitted. Bold values represent significant effects ($P < 0.05$) with (**) and without (*) Bonferroni adjustment for species composition by a permutation test.

767

768 **Figure legends**

769 Fig. 1. Locations of (a) the Yura River, (b) research area and (c) sampling sites. (d) Arrangement of
770 transects and plots.

771

772 Fig. 2. Longitudinal distribution pattern of fishes. (a) Fishes mainly distributed in the upper area.
773 (b) Fishes mainly distributed in the upper-middle area. (c) Fishes mainly distributed in the
774 lower-middle area. (d) Fishes mainly distributed in the lower area. Some rare species are omitted
775 for simplicity. The number of observed individuals was adjusted to a maximum of 1 by dividing
776 the maximum number of observed individuals among the sampling sites for each fish species.

777

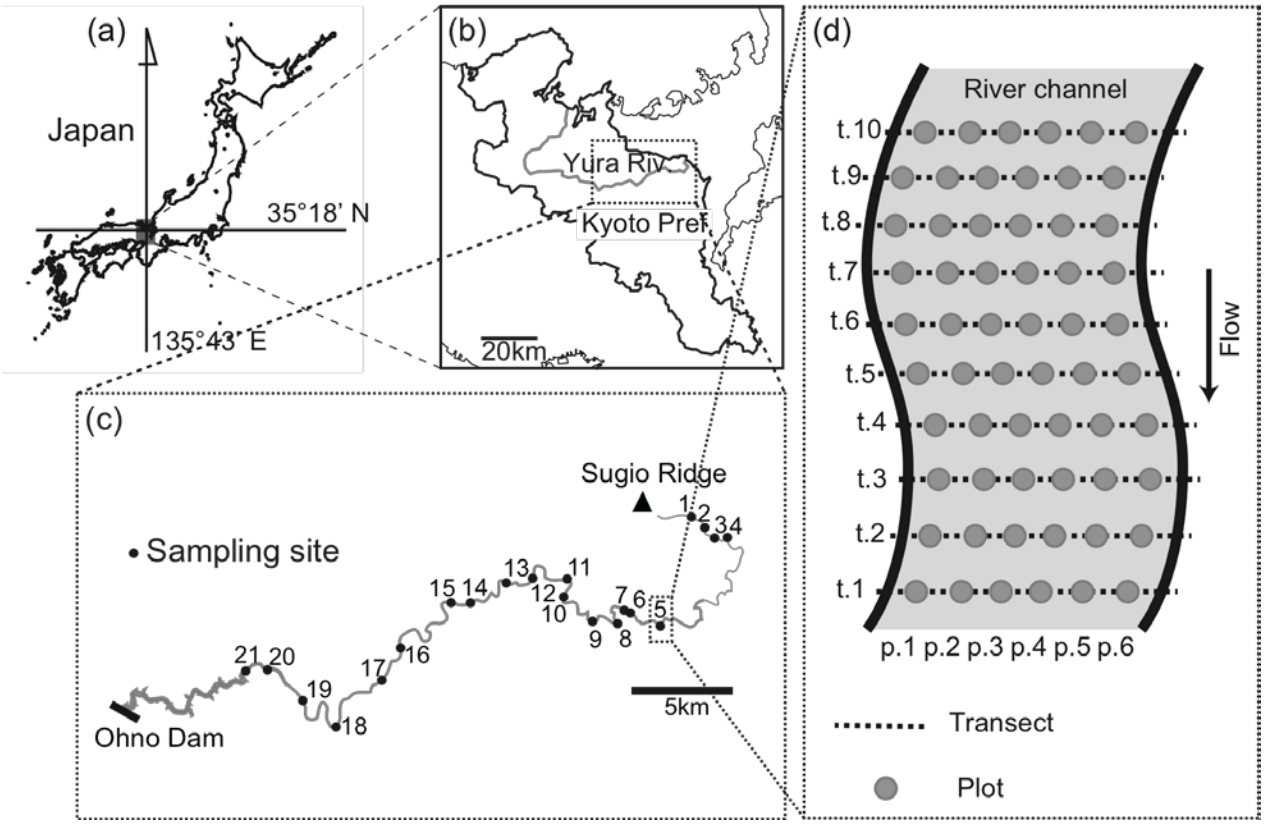
778 Fig. 3. Distance–similarity relationships in species composition and habitat environment at the
779 medium and fine spatial scales. In each figure, values represent the similarity of a given pair of
780 sites (medium scale) or plots (fine scale). The displayed curve is a running median with a sampling
781 proportion of 0.5. At the fine scale, similarities between <5 m and >50 m distant plots were
782 eliminated from the analysis because they did not exist in common at all sampling sites.

783

784 Fig. 4. Ordinations of Moran's eigenvectors (MEVs) 1, 2 and 3 along the river course that were
785 significantly correlated with the distribution pattern of fishes at the medium scale, obtained for a

786 spatial weighting matrix calculated using the approximate spatial structure of the arrangement of
787 sampling sites.
788
789 Fig. 5. Mappings of Moran's eigenvectors (MEVs) 2, 4 and 45 along the river course that were
790 significantly correlated with the distribution pattern of fishes at the fine scale, obtained for a
791 spatial weighting matrix calculated using the approximate spatial structure of the arrangement of
792 sampling plots at sites 5–13 and 15–19.
793

Figure 1 (Nakagawa, H)



794

Figure 2 (Nakagawa, H)

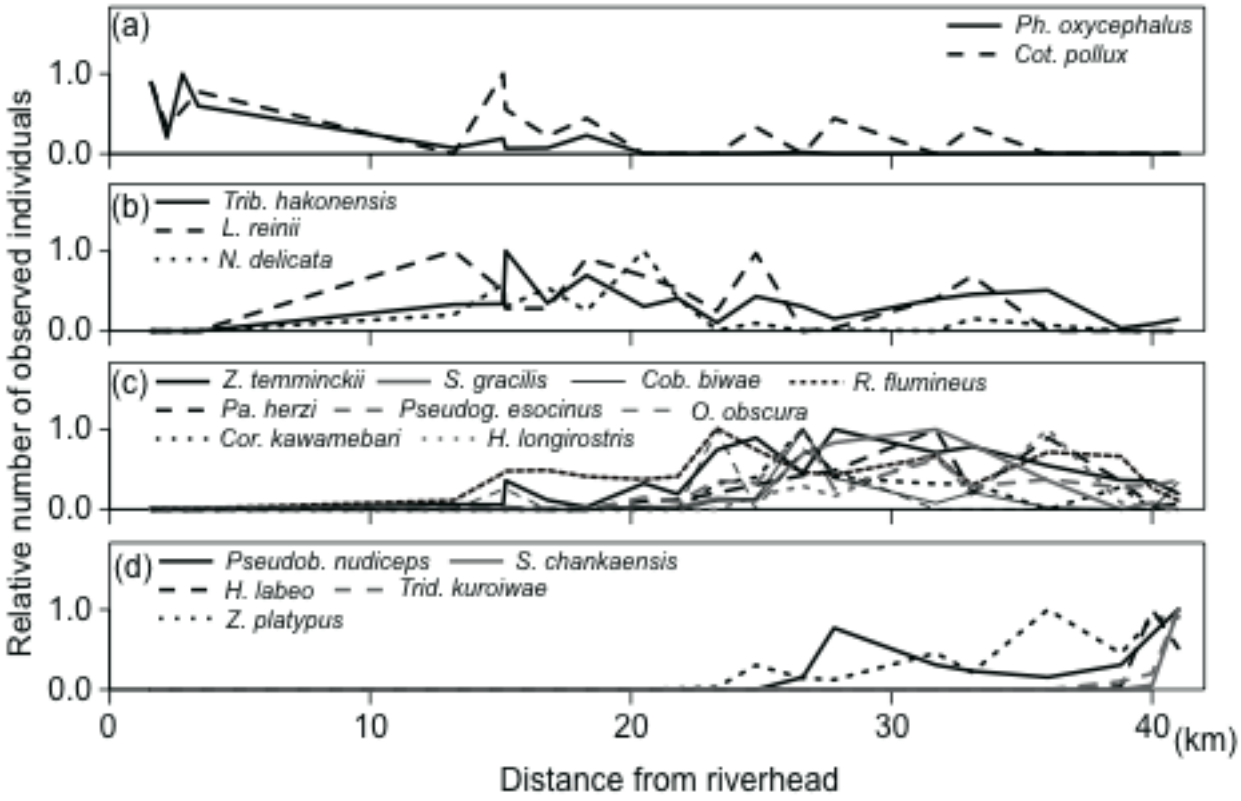


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Figure 3 (Nakagawa, H)

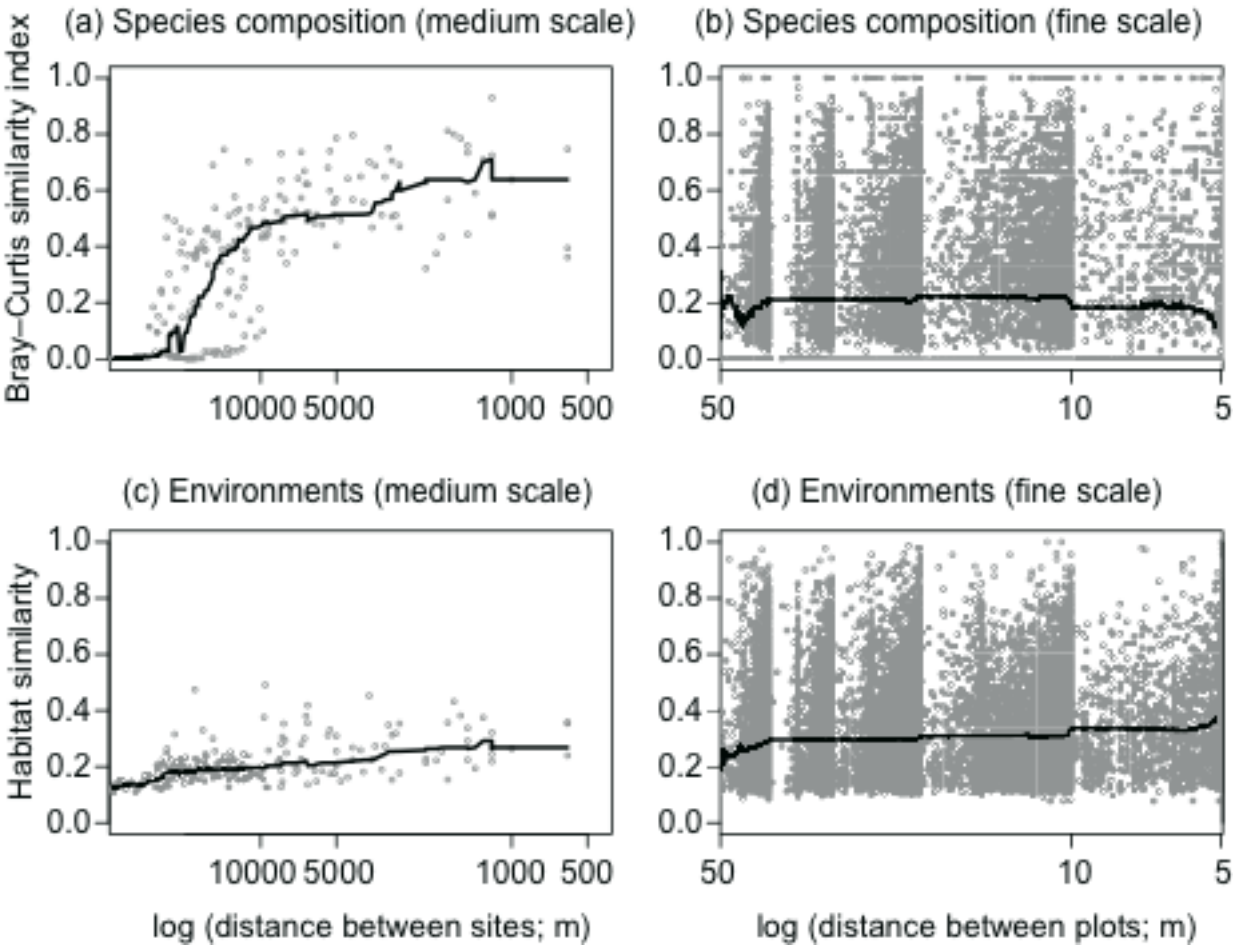

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Figure 4 (Nakagawa, H)

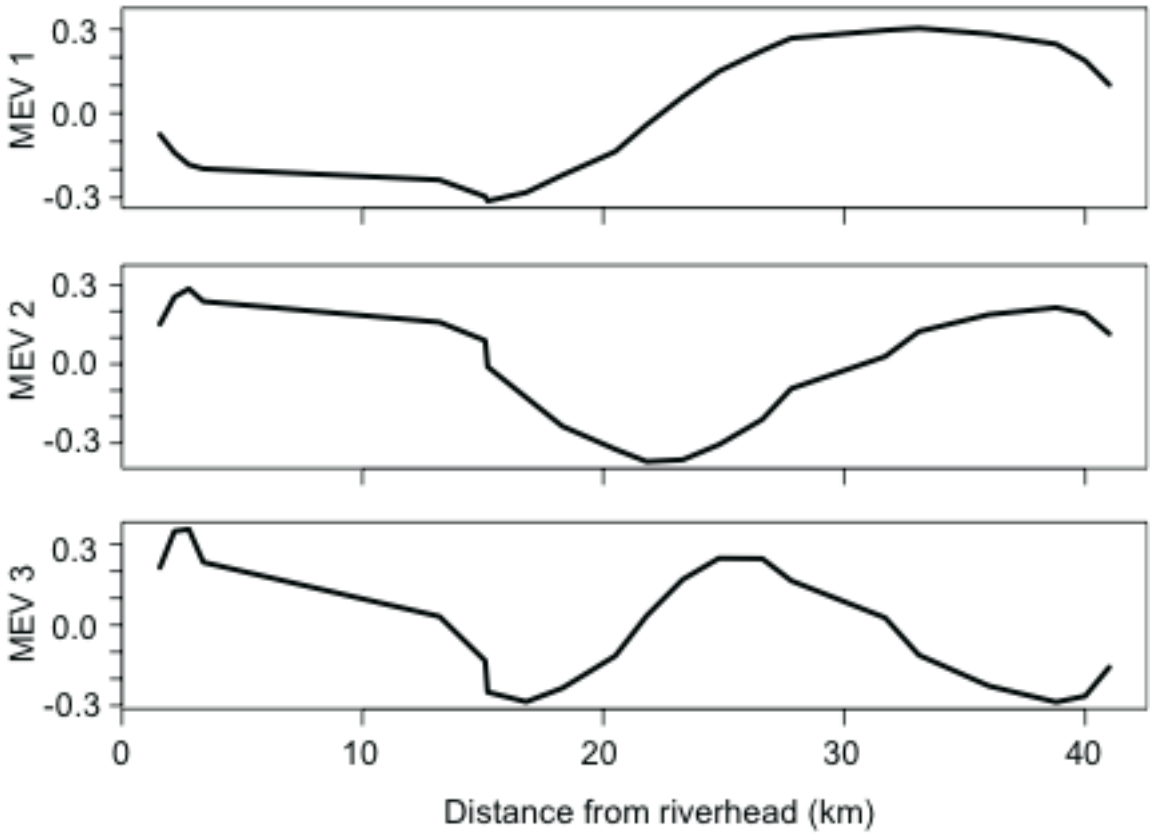

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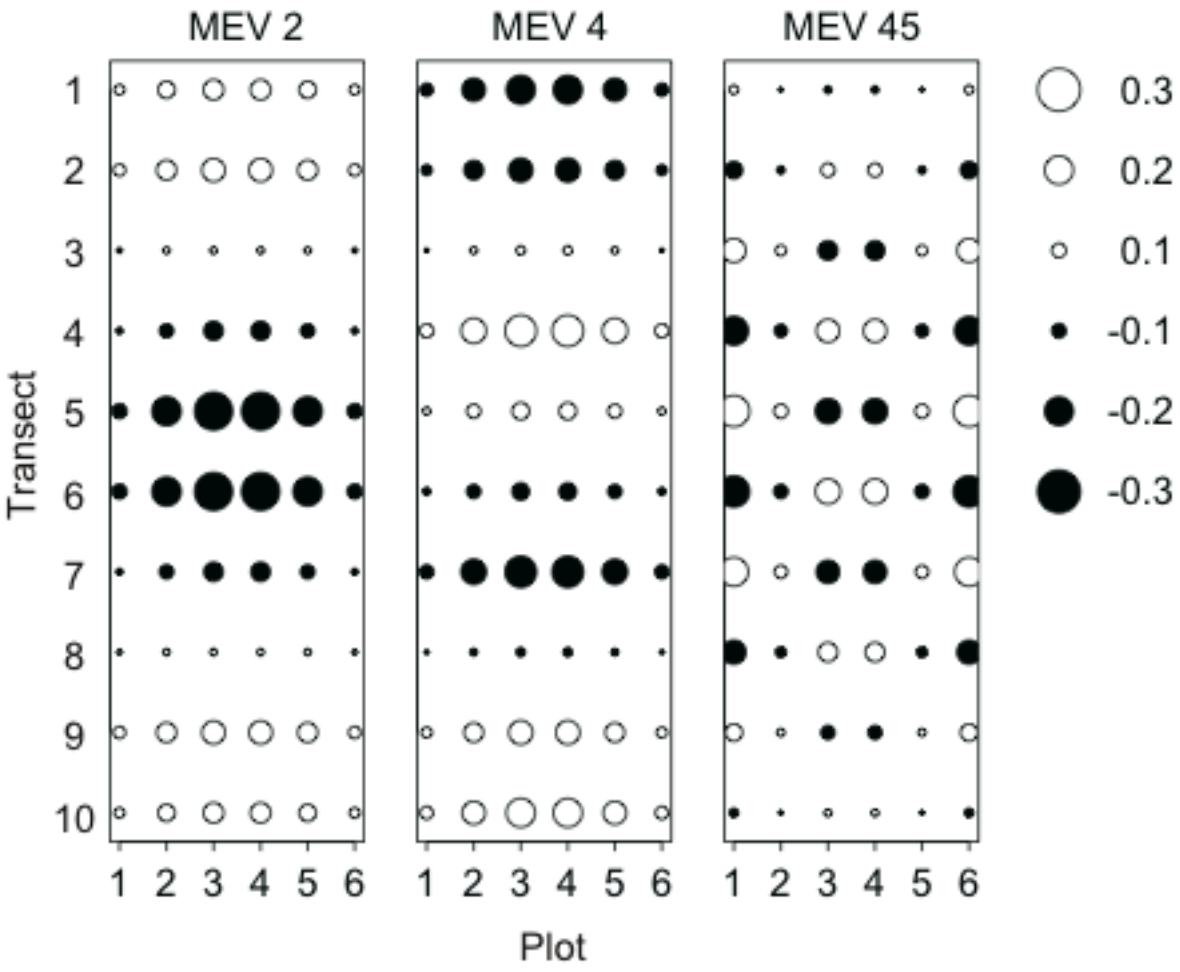
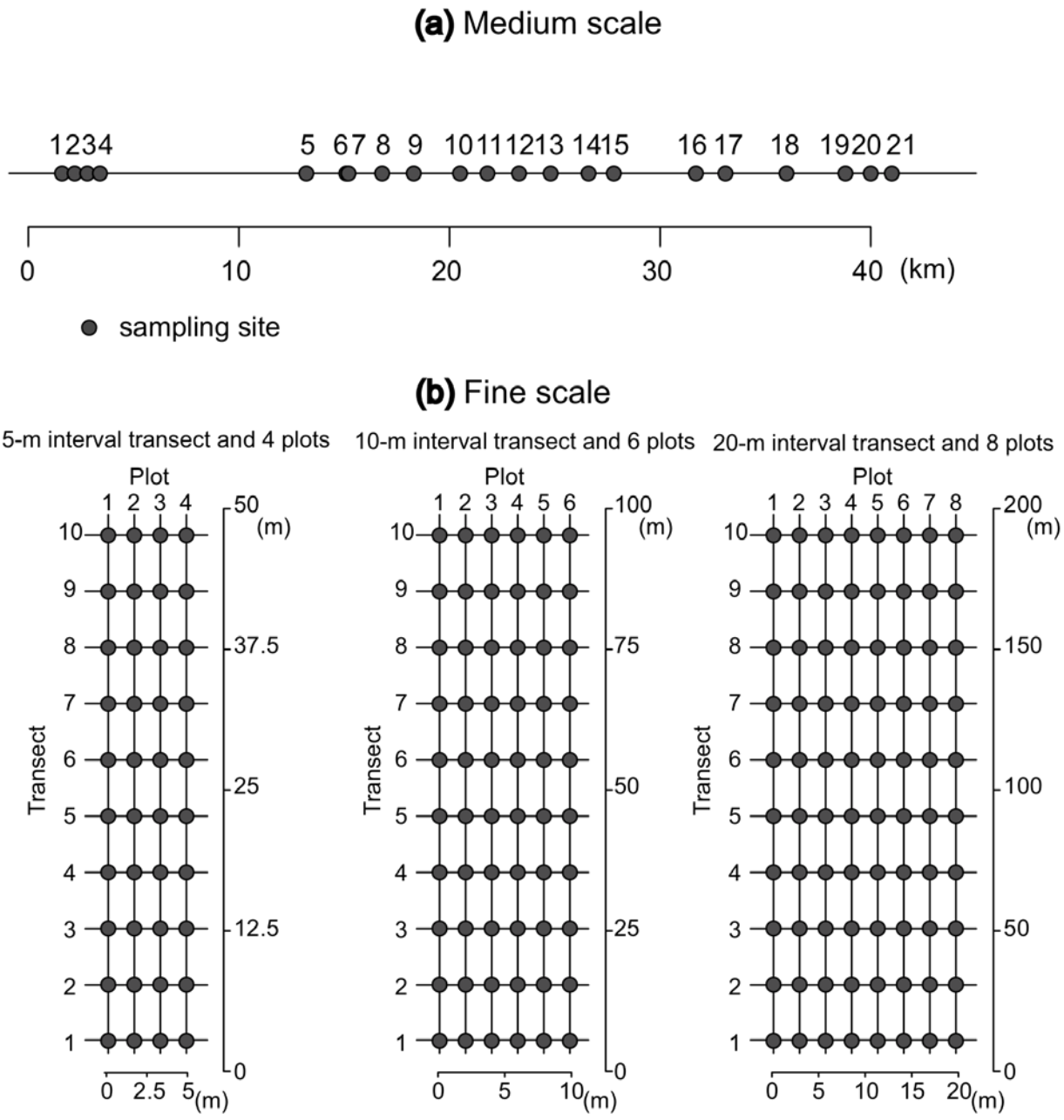
Figure 5 (Nakagawa, H)



798

799

800 **Appendix 1**



801

802 Appendix 1. Approximated spatial structure of the community and arrangement of sampling sites

803 and plots. (a) The spatial structure at the medium scale that approximated a 1-dimensional

804 structure. (b) The spatial structure at the fine scale that approximated a grid structure (see

805 Materials and methods for details).

806 **Appendix 2**

807 Appendix 2. Observed number of individuals of each fish species at each sampling site.

Species \ Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	day	night	Total
Oncorhynchus masou *1	2	2	4	1	3	0	0	1	9	0	2	0	0	0	0	0	0	0	0	0	0	12	12	24
Cottus pollux	8	3	5	7	0	9	5	2	4	0	0	0	3	0	4	0	3	0	0	0	0	1	52	53
Phoxinus oxycephalus	157	36	177	106	13	34	12	13	41	1	0	0	1	4	0	0	0	1	0	0	0	336	260	596
Liobagrus reinii	0	0	0	0	32	16	9	9	29	22	17	8	31	0	1	13	22	0	0	0	0	5	204	209
Niwaella delicata	0	0	0	0	25	72	37	67	31	124	51	1	12	0	2	0	19	9	0	0	0	359	91	450
Tribolodon hakonensis	0	0	0	0	39	40	118	41	82	36	48	12	51	36	18	47	54	60	4	10	17	592	121	713
Zacco temminckii	0	0	0	0	11	10	62	20	5	56	33	128	154	78	172	122	135	94	63	61	34	564	674	1238
Rhinogobius flumineus	0	0	0	0	40	178	189	193	161	147	161	405	297	183	170	263	118	285	263	100	40	3017	176	3193
Odontobutis obscura	0	0	0	0	0	1	1	0	0	0	0	4	0	3	2	0	0	0	0	0	0	3	8	11
Plecoglossus altivelis *1	0	0	0	0	1	0	1	0	4	9	16	3	3	8	5	23	10	7	0	1	1	77	15	92
Pangtungia herzi	0	0	0	0	1	1	2	0	0	7	8	14	21	29	33	68	14	61	24	3	5	151	140	291
Hemibarbus longirostris	0	0	0	0	0	0	0	0	0	1	0	0	4	7	4	17	4	24	2	0	0	13	50	63
Squalidus gracilis	0	0	0	0	0	0	0	0	0	1	1	5	4	25	30	36	29	13	0	3	0	86	61	147
Pseudogobio esocinus	0	0	0	0	0	0	1	0	0	12	7	29	26	80	20	50	23	30	22	24	29	48	305	353
Zacco platypus	0	0	0	0	0	0	2	3	0	2	5	11	119	56	48	179	85	392	177	347	355	1207	574	1781
Coreoperca kawamebai	0	0	0	0	0	0	0	0	0	0	0	8	10	25	10	8	8	0	7	0	2	53	25	78
Cobitis biwae	0	0	0	0	0	0	0	0	0	1	0	4	5	38	15	3	8	1	0	0	13	43	45	88
Pseudobagrus nudiceps	0	0	0	0	0	0	0	0	0	0	0	0	0	2	10	4	3	2	4	9	13	4	43	47
Hemibarbus labeo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	27	14	37	5	42
Lepomis macrochirus *2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	0	2
Squalidus chankaensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	18	6	13	19
Tridentiger kuroiwae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	10	11	2	13
Chaenogobius urotaenia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	0	6	6
Rhinogobius sp. OR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	1	6	1	7
Anguilla japonica *1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	2
Cyprinus carpio	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1
Carassius carassius	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1
Total	167	41	186	114	165	361	439	349	366	419	349	632	741	575	545	833	535	985	568	593	557	6635	2885	9520

808

809 *1 Artificially introduced by local fisheries.

810 *2 Invasive species from North America.

811

812 **Appendix 3**

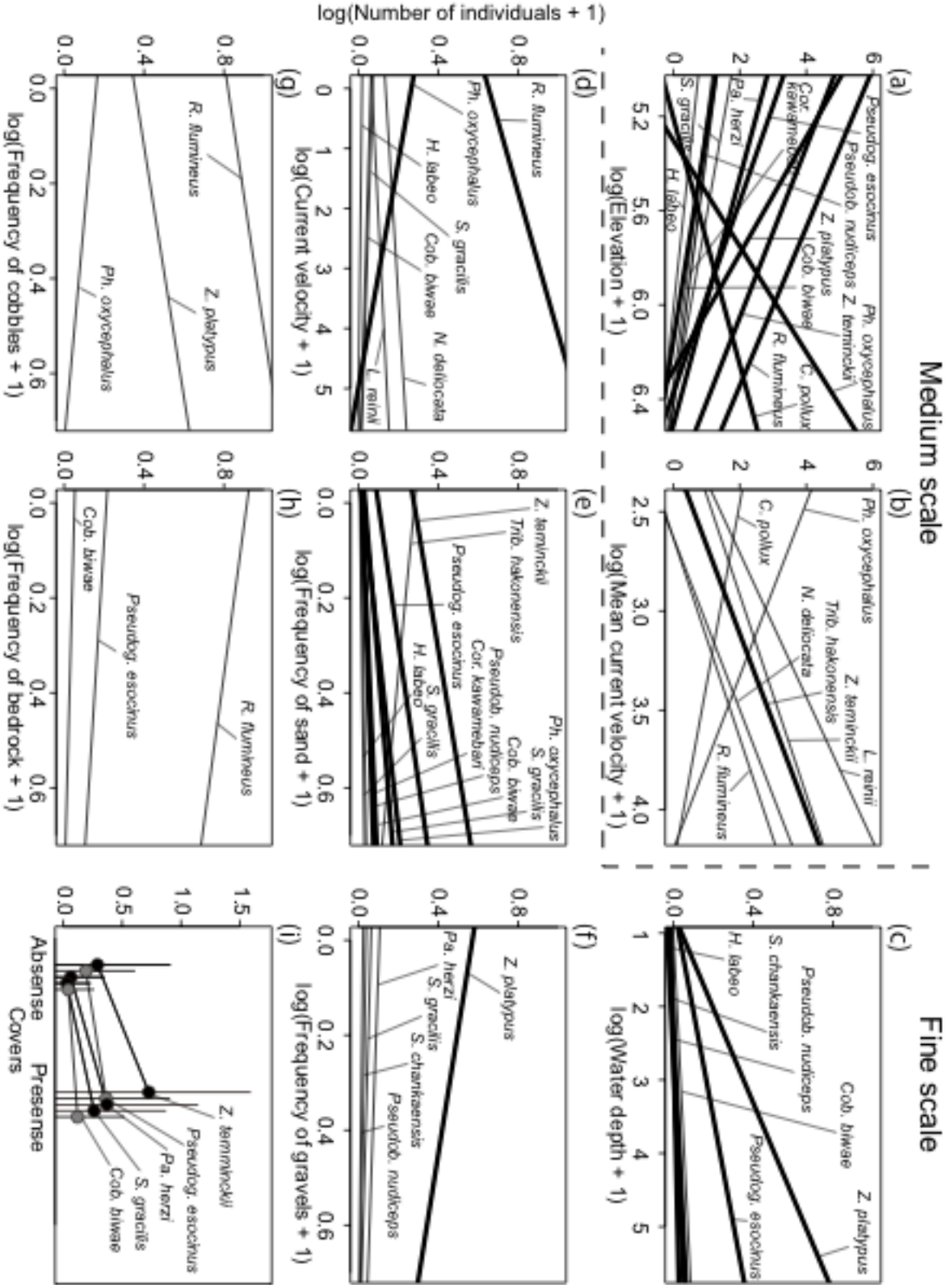
813 Appendix 3. Mean ± SD of environmental factors at each sampling site.

Sampling site	Elevation (m)	Water temperature (℃)	Gradient of riverbed (%)	Flow rate (m^3/s)	River width (m)	Water depth (cm)	Current velocity (cm/s)	Frequency of each substrate type (%)					Presence/absence of covers (0 or 1)
								Sand	Gravel	Cobble	Boulder	Bed rock	
1	650	14.8	0.03	0.05	3.0 ± 1.4	17.4 ± 16.4	10.5 ± 12.2	0.06 ± 0.21	0.61 ± 0.31	0.20 ± 0.18	0.01 ± 0.03	0.13 ± 0.32	0.03 ± 0.16
2	640	15.0	0.02	0.12	4.0 ± 1.5	11.5 ± 6.9	25.2 ± 23.2	0.04 ± 0.08	0.58 ± 0.24	0.22 ± 0.16	0.13 ± 0.15	0.03 ± 0.13	0.03 ± 0.16
3	630	15.0	0.02	0.19	4.8 ± 1.7	19.3 ± 17.4	25.4 ± 56.9	0.23 ± 0.38	0.41 ± 0.34	0.15 ± 0.20	0.01 ± 0.03	0.20 ± 0.29	0.00 ± 0.00
4	620	15.0	0.02	0.15	5.4 ± 1.0	27.5 ± 19.0	10.5 ± 15.8	0.04 ± 0.08	0.52 ± 0.31	0.19 ± 0.17	0.03 ± 0.08	0.23 ± 0.35	0.03 ± 0.16
5	400	19.2	0.02	1.14	5.8 ± 1.1	57.4 ± 32.5	38.8 ± 32.3	0.01 ± 0.04	0.37 ± 0.34	0.15 ± 0.18	0.17 ± 0.20	0.30 ± 0.37	0.00 ± 0.00
6	370	19.8	0.01	0.88	11.6 ± 3.7	32.3 ± 31.8	25.3 ± 26.7	0.06 ± 0.18	0.51 ± 0.35	0.24 ± 0.23	0.04 ± 0.09	0.16 ± 0.35	0.03 ± 0.18
7	370	19.9	0.01	1.09	11.0 ± 3.3	32.6 ± 24.6	35.1 ± 42.9	0.04 ± 0.12	0.50 ± 0.33	0.26 ± 0.24	0.14 ± 0.22	0.06 ± 0.19	0.03 ± 0.17
8	350	20.4	0.01	0.91	9.6 ± 2.9	49.9 ± 42.5	20.5 ± 27.1	0.06 ± 0.15	0.63 ± 0.33	0.18 ± 0.19	0.00 ± 0.02	0.13 ± 0.31	0.00 ± 0.00
9	320	20.6	0.02	0.83	9.4 ± 2.1	27.6 ± 17.0	34.8 ± 31.9	0.02 ± 0.08	0.44 ± 0.24	0.41 ± 0.20	0.12 ± 0.15	0.00 ± 0.00	0.00 ± 0.00
10	300	19.4	0.01	1.83	12.6 ± 4.6	53.3 ± 44.4	29.7 ± 32.1	0.03 ± 0.13	0.71 ± 0.30	0.17 ± 0.18	0.01 ± 0.03	0.08 ± 0.26	0.00 ± 0.00
11	290	19.2	0.01	1.84	11.6 ± 3.4	33.3 ± 29.6	50.6 ± 40.8	0.03 ± 0.12	0.64 ± 0.31	0.23 ± 0.22	0.02 ± 0.09	0.08 ± 0.25	0.00 ± 0.00
12	280	19.0	0.00	0.87	15.5 ± 2.0	25.1 ± 16.2	24.8 ± 22.4	0.08 ± 0.17	0.66 ± 0.27	0.20 ± 0.20	0.02 ± 0.07	0.03 ± 0.15	0.00 ± 0.00
13	280	18.3	0.01	1.19	13.1 ± 3.0	28.5 ± 18.4	33.6 ± 22.8	0.08 ± 0.16	0.49 ± 0.25	0.31 ± 0.21	0.06 ± 0.11	0.06 ± 0.21	0.00 ± 0.00
14	260	20.5	0.01	2.27	35.8 ± 12.6	62.8 ± 39.4	11.9 ± 7.3	0.18 ± 0.34	0.69 ± 0.39	0.05 ± 0.09	0.00 ± 0.02	0.08 ± 0.26	0.08 ± 0.27
15	250	19.2	0.01	2.02	12.3 ± 3.8	71.0 ± 36.4	27.8 ± 18.2	0.18 ± 0.29	0.53 ± 0.36	0.11 ± 0.14	0.03 ± 0.12	0.16 ± 0.31	0.27 ± 0.45
16	220	19.9	0.01	1.68	19.8 ± 2.5	42.9 ± 31.7	21.5 ± 22.2	0.16 ± 0.26	0.34 ± 0.26	0.31 ± 0.22	0.10 ± 0.14	0.08 ± 0.20	0.03 ± 0.18
17	200	20.0	0.01	3.62	13.9 ± 3.0	67.4 ± 42.4	44.0 ± 37.1	0.06 ± 0.19	0.34 ± 0.31	0.26 ± 0.26	0.06 ± 0.14	0.27 ± 0.35	0.05 ± 0.22
18	190	20.7	0.01	1.91	17.4 ± 3.2	35.7 ± 16.6	34.1 ± 27.6	0.02 ± 0.08	0.26 ± 0.27	0.34 ± 0.27	0.11 ± 0.19	0.27 ± 0.38	0.00 ± 0.00
19	170	20.8	0.01	2.22	19.2 ± 2.3	38.6 ± 33.2	31.8 ± 28.1	0.04 ± 0.17	0.71 ± 0.34	0.12 ± 0.15	0.02 ± 0.06	0.12 ± 0.29	0.00 ± 0.00
20	160	20.7	0.00	3.50	25.9 ± 3.8	44.9 ± 27.8	33.2 ± 31.2	0.07 ± 0.19	0.43 ± 0.29	0.35 ± 0.25	0.06 ± 0.11	0.09 ± 0.23	0.00 ± 0.00
21	160	19.5	0.01	3.53	24.1 ± 3.5	90.9 ± 60.3	18.3 ± 20.0	0.11 ± 0.26	0.46 ± 0.39	0.21 ± 0.28	0.07 ± 0.16	0.15 ± 0.32	0.00 ± 0.00

814

815

816 **Appendix 4**



817

Appendix 4. Relationships between environmental factors and the number of observed individuals at medium (a), (b) and fine (c)–(i) scales. Fish species for which the total number of observed individuals was <20 are omitted. In (a)–(h), lines show significant regression lines with and without Bonferroni adjustment between environmental factors and the observed number of individuals of each species. Line types show the significance of correlation by linear regression: thin lines indicate $P < 0.05$ and bold lines indicate $P < 0.05$ with Bonferroni adjustment. In (i), circles show means and bars denote the SDs for each species. Black and grey circles indicate the existence of a significant difference with $P < 0.05$ with and without Bonferroni adjustment, respectively, by ANOVA testing.